

COMPARISON OF OLD AND NEW WORLD *ACANTHAMETROPUS* (EPHEMEROPTERA: ACANTHAMETROPODIDAE) AND OTHER PSAMMOPHILOUS MAYFLIES^{1, 2}

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ABSTRACT: The first comparative examination of larvae of the psammophilous mayfly genus *Acanthametropus* from throughout its known Holarctic range substantiated the present classification that recognizes two species, *A. pecatonica* (Burks) from eastern North America and *A. nikolskyi* Tshernova from eastern Eurasia. Mature larvae of the two species may be differentiated on the basis of the series of sharp hooklike projections on the venter of the abdomen of *A. nikolskyi* vs. the much less developed homologous projections on the abdomen of *A. pecatonica*. Spines and processes on the head, thorax, and dorsal abdomen of larvae apparently become more pronounced with age. Similarities between Acanthametropodidae and certain other psammophilous mayfly taxa include Northern Hemisphere vicariant biogeographic patterns, predatory habits, crablike walking, speed-swimming, and low numbers of species. The relative rarity and restricted habitats of these highly specialized mayflies underscore the need for conserving riverine habitats.

Acanthametropus is a little-known Holarctic genus of mayflies that was not discovered until the mid-twentieth century (Tshernova 1948). Larvae of *Acanthametropus* develop in rivers where they are predatory and psammophilous, living on noncohesive sand substrates. Because such habitats tend to have limited and specialized benthic macroinvertebrate communities that are low in diversity [see e.g., Hynes (1970), Barton and Smith (1984), and Minshall (1984)], they tend to be neglected by ecologists and general collectors. The rarity of *Acanthametropus* and several other psammophilous mayflies in collections is at least in part a result of this. In addition, however, if *Acanthametropus* larvae are elusive speed-swimmers, as I predict, that would further explain this rarity.

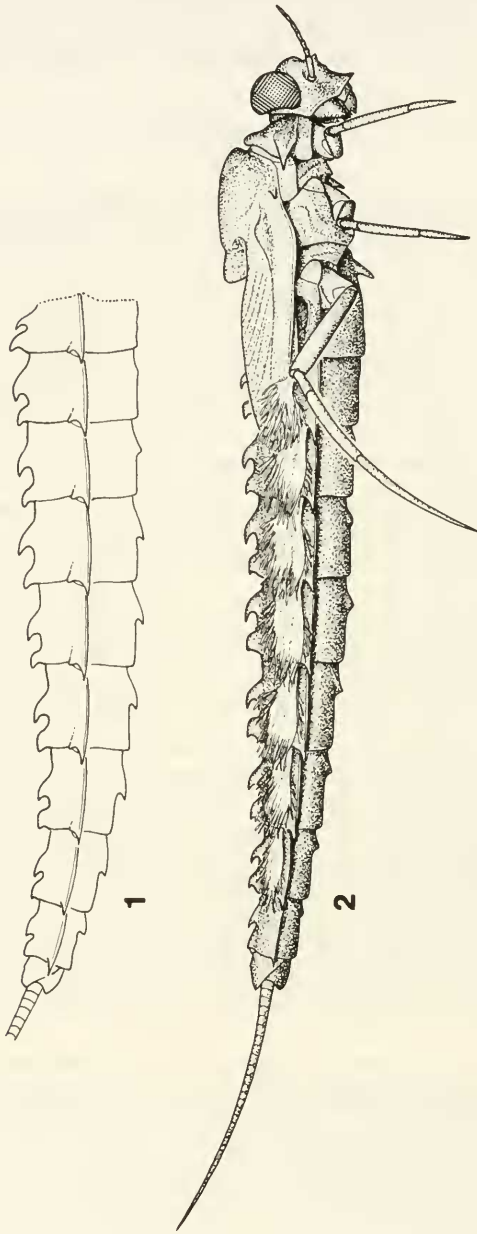
Only two species of *Acanthametropus* have been named: *A. nikolskyi* Tshernova (1948) is known from the Amur Basin, eastern USSR, and *A. pecatonica* (Burks 1953) is known from the midwestern USA (northern Illinois and Wisconsin) and southeastern USA (Georgia and South Carolina). The adult stage of *A. nikolskyi* has been known since 1970 (Bajkova 1970, Tshernova *et al.* 1986); however, attempts to find adults or rear larvae in North America have thus far been unsuccessful (Lillie *et al.* 1987).

The enigmatic larval characterization of *Acanthametropus* [see Fig. 312, labeled *Metreturus* in Burks (1953) for dorsal habitus and Figs. 1 and

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Figs. 1-2. *Acanthametropus* mature larvae, lateral view. 1. *A. nikolskyi*, abdominal profile. 2. *A. peatonica* (holotype, 25.3 mm long), detailed habitus.

2 herein for lateral habitus] led Edmunds, in Edmunds *et al.* (1963), to place the genus in a separate subfamily Acanthametropodinae of the family Siphonuridae. The additional inclusion of three other genera (*Analetris* Edmunds, *Siphuriscus* Ulmer, and *Stackelbergisca* Tshernova) in that subfamily was discussed by Edmunds and Koss (1972). Demoulin (1974) restricted the subfamily to include *Acanthametropus* exclusively, and McCafferty (1991) has given familial rank to that latter taxonomic concept.

The number and characterization of species in *Acanthametropus* has not been adequately addressed. Edmunds *et al.* (1976) indicated that there were some differences in Illinois and South Carolina specimens but that it could not be determined whether or not the differences were of a specific nature or due to relative age of the larvae. In addition, the known larvae from Eastern and Western Hemispheres have not previously been brought together and compared to determine if indeed different species are represented. This question is germane because several Ephemeroptera populations historically thought to represent Nearctic and Palearctic species or species pairs have recently been shown to represent single circumpolar species (e.g., see McCafferty 1985, Flowers 1986). If more than one species is involved, differentiating characterization would be important to note.

The only fully mature larval specimen taken thus far in the USA is the holotype of *A. pecatonica* from the Sugar River in Illinois. A slightly younger specimen has recently been taken in the Wisconsin River, Wisconsin. The above mentioned holotype larva is comparable in size with the most mature specimen currently known from the USSR, which was taken near the type locality of *A. nikolskyi* in the Amur River, Siberia. I have examined the above specimens as well as early and middle instar larvae of *Acanthametropus* from the Flint River in Georgia, the Savannah River in South Carolina, and the Wisconsin River in Wisconsin.

Based on this comparative study, I am able to substantiate that there is one species in eastern North America and one species in eastern Eurasia. The most obvious difference in the larvae of *A. pecatonica* and *A. nikolskyi* is the relative development of the posteromedial projections on each of the abdominal sternites (Figs. 1 and 2). These projections are most developed on segments 4-8 in both species. However, whereas the projections are evident and somewhat bluntly conical in *A. pecatonica* (Fig. 2), they are sharp, spinelike, and hooked posteriorly in *A. nikolskyi* (Fig. 1). Other spination of the head, thorax, and abdomen (see especially the dorsal abdomen) is virtually identical in the mature larval specimens of the two species. There may be some specific difference in the relative development of fibrillae on the gill lamellae (appearing somewhat more profuse in *A. pecatonica*), but this character is difficult to quantify without more specimens.

In *A. pecatonica*, the relative development of spination changes slightly with age. Generally, the spines become larger, more sclerotized, and more defined as the larvae develop. If this is also true for *A. nikolskyi*, it could possibly mean that the ventral abdominal projection characterization for the two species may be less pronounced when comparing young larvae. No early instar larvae of *A. nikolskyi* were available to test this supposition; however, from the lateral drawing of the evidently very early instar type of *A. nikolskyi* (wingpads are not even apparent in the accompanying dorsal drawing) that was provided by Tshernova (1948), no ventral abdominal armature was indicated.

Although preliminary, presentation of the above conclusions at this time is justifiable because there is no prospect that any appreciable additional materials for more intensive study will become available in the near future.

Comparisons With Other Psammophilous Mayflies

Besides Acanthametropodidae, psammophilous mayfly taxa include the Behningiidae (Keffermüller 1963, McCafferty 1975), Metretopodidae (Lyman 1956; McCafferty, unpublished), Analetrididae (Edmunds and Koss 1972), Ametropodidae (Allen and Edmunds 1976, Clifford and Barton 1979), and Pseudironidae (Barton 1980, Pescador 1985). All but the Behningiidae were placed in the infraorder Arenata by McCafferty (1991); the affinity of Behningiidae is with the Leptophlebioidea and Ephemeroidea in the infraorder Lanceolata. Certain genera in other families unrelated to the Acanthametropodidae have also been associated with sand substrates. These include, for example, *Homoeoneuria* (Pescador and Peters 1980) and presumably *Oligoneurisca* in the Oligoneuriidae; some species of *Brachycercus* (Spieth 1938, Peters and Jones 1973), *Amercaenis* (Provonsha and McCafferty 1985), and *Clypeocaenis* (McCafferty, unpublished) of the Caenidae; some species of *Centropilum* (McCafferty and Waltz 1990), *Demoulinia* (McCafferty, unpublished), *Potamocloeon* (Gillies 1990), and *Pseudocentropiloides* (Keffermüller and Sowa 1984) of the Baetidae; and some species of *Baetisca* (Hilsenhoff 1975, 1984; Edmunds 1977) of the Baetiscidae.

The psammophilous mayflies mentioned above, with the exception of some Metretopodidae (Lyman 1956), are lotic. They have variously been reported from shifting sand, sand bars, thin layers of silt overlying sand, and marginal sand at the edge of finer or coarser substrates. Although the sand is generally noncohesive, in some cases it apparently grades to silt/sand that can be somewhat compacted. It should be pointed out, however, that in some of the reports of habitat, descriptions of the sand

are qualitative or even anecdotal, and the precise habitat or the exact condition of sand in a habitat have seldom been quantified. In some cases, mature larvae may leave the sandy habitat just prior to emergence; for example, in the *Metretropodidae*, mature larvae become climbers in marginal vegetation prior to emergence (Lehmkuhl 1970, Hilsenhoff *et al.* 1972) and as a result have mostly been collected there.

Certain burrowing mayflies, such as species of *Anthopotamus* (Bae and McCafferty, in manuscript) in the *Potamanthidae*, *Ephemera* (Eriksen 1968) in the *Ephemeridae*, and *Ephoron leukon* (McCafferty, unpublished) in the *Polymitarcyidae* may be found associated with substrate containing sand, but the sand is heavily mixed with silt or gravel, or both. I do not consider them psammophilous. Still other mayfly taxa, such as *Apobaetis* and *Paracloeodes* of the *Baetidae*, are supposedly psammophilous (see Day 1955), but additional ecological data are needed to confirm their habitat.

Many psammophilous mayfly taxa demonstrate adaptations similar to those of the *Acanthametropodidae*. Predominant feeding adaptations of psammophilous mayflies include predation, passive filter feeding, and foraging fine detritus and periphyton from the sand substrate itself. The predatory habit, which has been considered relatively uncommon among mayflies in general (e.g., Edmunds 1957), is well represented in sand-dwelling mayflies, and sand-dwelling midges are evidently an abundant food source for such predators. In addition to the *Acanthametropodidae*, predatory psammophilous mayflies include the *Behningiidae* (Tsui and Hubbard 1979), *Analetrididae* (Edmunds and Koss 1972), and *Pseudironidae* (Soluk and Craig 1990). Passive filter feeding is present in the *Ametropodidae* (Soluk and Craig 1988), the psammophilous *Oligoneuriidae* (Edmunds *et al.* 1976), and presumably *Amercaenis* (Provonsha and McCafferty 1985) and *Clypeocaenis* (Soldán 1978). The other psammophilous mayflies mentioned above are bottom-feeding microvores (Aro 1910, Pescador and Peters 1974, Clifford 1976, Chaffee and Tarter 1979, Hamilton and Clifford 1983, Soldán 1986).

Above, I predicted that *Acanthametropus* larvae would be elusive and difficult to collect even when populations could be located. This is because other psammophilous mayflies of the infraorder *Arenata* are exceptionally swift swimmers (Leonard and Leonard 1962, Edmunds and Koss 1972, Allen and Edmunds 1976, Soluk and Clifford 1984, McCafferty and Provonsha 1986); *Analetrididae* (Edmunds and Koss 1972) and *Pseudironidae* (McCafferty and Provonsha 1986), at least, must literally be herded into very broad or deep nets since they easily escape standard kick screens. Barton and Smith (1984) have also commented on the inherent difficulty of collecting psammophilous mayfly populations.

Of the Arenata, the Acanthametropodidae, Pseudironidae, and Analetrididae have similar crablike legs, with long, somewhat curved, uniform tarsi and claws. The Pseudironidae have been seen to move deftly over the sand backwards and sideways just as sand crabs move (McCafferty and Provonsha 1986). Edmunds and Koss (1972) noted that Analetrididae could move backwards and forwards on the sand but provided no other details. Presumably, Analetrididae and Acanthametropodidae also move crablike. Ametropodidae and Metretopodidae have modified forelegs, but their middle and hindlegs have long slender claws that may enable them to move somewhat similarly on sand substrates. Details of movement in other psammophilous mayflies are not generally known, although it is known that the Behningiidae live interstitially within the sand (McCafferty 1975) and do not show any adaptations for proficient swimming or running. Legs and claws of psammophilous mayflies such as some *Brachycercus*, *Homoeoneuria*, and certain baetids are quite unlike those of any Arenata; they possess needlelike claws that may serve to help anchor them in sand.

Many psammophilous mayflies, particularly those that are predatory, have an Amerasian distribution pattern similar to that seen in Acanthametropodidae. The Behningiidae, for example, although unrelated, shows a similar Holarctic pattern, although it is a bit more widespread in the Palearctic, which is probably due to the fact that it is more radiated (with three genera) than Acanthametropodidae. (The nonpredatory groups Ametropodidae and Metretopodidae are also Holarctic but with ranges including western North America and western Eurasia.)

In North America, distribution patterns of the predatory, psammophilous mayfly species tend to be broadly disjunct and to involve the upper Osage and Great Plains in central North America and the Southeastern Coastal Plains. Unique characteristics of these systems and pertinent aspects of their general ecology have been treated, for example, by Patrick *et al.* (1966), Peters and Jones (1973), Barton and Lock (1979), and Matthews (1988). Disjunctions similar to the distribution of *Acanthametropus pecatonica* given above are found in *Dolania americana* (Behningiidae) (Edmunds *et al.* 1976, Jacobs 1990) and *Pseudiron centralis* (Pseudironidae) (Pescador 1985). Such disjunctions are probably a function of vicariance, related to the geologic events that have affected the continuity of drainage systems providing adequate sand habitats.

The predatory, riverine mayflies *Raptoheptagenia cruentata* (Heptageniidae: Heptageniinae), and *Anepeorus simplex* (Heptageniidae: Anepeorinae) [see McCafferty and Provonsha (1988) for the current nomenclatural application of these names] have a basically similar North American distribution pattern. Any possible ecological relationship with sand

substrates in these predatory heptageniids is not clear at this time since they have been predominantly taken in deep drift and dredge samples. However, Edmunds *et al.* (1976) stated that *Raptoheptageniä* larvae [incorrectly known as *Anepeorus* larvae at that time] "show a preference for rocks over sand substrate, and they move very rapidly."

Similar to *Acanthametropus*, the other predatory, psammophilous mayfly genera are all relatively very distinct and evidently monospecific in North America. Those that are Holarctic consist of only a very few species. This perhaps indicates an old origin but low rate of speciation. They are also restricted to the Northern Hemisphere, and some lineages of Arenata are possibly of Laurasian origin. Of the other taxa having psammophilous mayflies, Baetiscidae is restricted to the Nearctic, but psammophilous baetids, caenids and oligoneuriids, are known from the Southern Hemisphere.

Given the many similarities among psammophilous mayflies, it is important to decipher which of the similarities reflect a common evolutionary ancestry and which are in fact parallelisms that have resulted from adaptations to similar environmental circumstances. Thus, the special ecological relationships as well as cladistics of these mayflies need to be carefully studied. I cannot be optimistic about such a prospect, however, because the actual survival of many of them may be in serious jeopardy.

McCafferty *et al.* (1990) stressed the need for conserving riverine habitats, citing in particular the rarity and specialized nature of psammophilous, riverine mayflies in North America and the fact that much of this habitat is already altered or threatened. For example, areas of the White River in Indiana that are unpolluted and have shifting sand substrates are disappearing (McCafferty, unpublished), many streams and rivers with shifting sand substrates in the Southeast, although relatively common, are disturbed (Peters and Peters 1977), and prairie streams, which are often typified by sandy substrates such as in the Platte system, are possibly "mere remnants of former systems, having been ravaged by pump, plow, and pollution" (Matthews 1988). The exploitation of U.S. rivers continues at an alarming rate, and natural riverine ecosystems in general continue to decline (see Benke 1989). This will have dire consequences for riverine mayflies that are psammophilous or predatory or both. For example, one such predatory and possible psammophilous species, *Anepeorus rusticus*, from the Green River in Utah is probably extinct and another, *Acanthomola pubescens*, from the Saskatchewan River may be nearly extinct as the result of regulating such rivers (see McCafferty and Provonsha 1985, Whiting and Lehmkuhl 1987, and McCafferty *et al.* 1990).

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